

U.S. DEPARTMENT OF THE INTERIOR
NATIONAL BIOLOGICAL SERVICE

BIOLOGICAL SCIENCE REPORT 2

EVALUATIONS OF DUCK
HABITAT AND
ESTIMATION OF DUCK
POPULATION SIZES
WITH A
REMOTE-SENSING-BASED
SYSTEM

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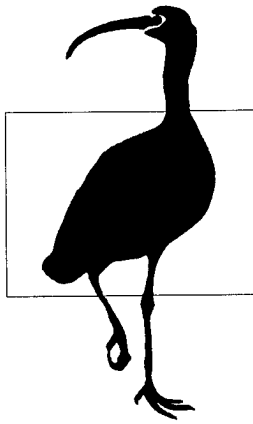
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By

Lewis M. Cowardin,

Terry L. Shaffer,

and

Phillip M. Arnold

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Evaluations of Duck Habitat and Estimation of Duck Population Sizes with a Remote-Sensing-Based System

by

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Abstract. During 1987–90, we used high-altitude photography, aerial videography, counts, and models to estimate sizes of breeding populations of dabbling ducks (Anatinae) and duck production and to identify duck habitat on U.S. Fish and Wildlife Service land and easements and on private land in the prairie pothole region of the United States. The study area contained about 3.1 million wetland basins (28,490 km²). Wetland area (ha per km²) was highest on service-owned land; wetland-basin density was greatest on service easements. Temporary and seasonal wetlands were underrepresented and lakes were overrepresented on service-owned land. Seventy-eight percent of all basins were less than 0.41 ha. Cropland dominated private land. Pond density decreased from 4.4/km² in 1987 to 3.4/km² in 1990 and pond area, from 7.2 ha/km² to 2.7 ha/km². The density of the blue-winged teal was greatest (3.4 pairs/km²) and was followed in magnitude by those of the mallard (2.1 pairs/km²), the gadwall (1.8 pairs/km²), the northern pintail (0.8 pairs/km²), and the redhead (0.8 pairs/km²). Duck density was consistently highest on service-owned land. The decline of breeding-population sizes in 1987–90 closely corresponded to losses of pond numbers and pond area. The density of breeding pairs per pond was inversely related to pond density, suggesting that breeding ducks tended to concentrate on the remaining ponds as drought intensified. The production of recruits followed the same pattern as breeding-population sizes. We estimated that 2.5% of the ducklings hatched on service-owned land, which was 1.3% of the study area; 19.6% hatched on service easements, which were 14.2% of the study area; and 77.9% hatched on private land, which was 84.6% of the study area. Various sources of bias and sampling error and improvements to the system are discussed.

Key words: Ducks, wetlands, population, recruitment, management, models, videography, drought.

The U.S. Fish and Wildlife Service has long been involved in monitoring wetland conditions and duck populations. Cooperative breeding-ground surveys by the United States and Canada (Martin et al. 1979; Reynolds 1987) have provided data essential to management of continental waterfowl populations. However, these surveys were designed for obtaining data that are used primarily for setting annual hunting regulations and were not intended for obtaining data for the management of national wildlife refuges and wetland management districts or for evaluating differences of habitat use by ducks among landownership classes.

To meet the unfilled need for data from local areas, Hammond (1969) developed a system for measuring duck use and production on refuges and in waterfowl production areas in the prairie pothole region of the United States. That

system was frequently modified to meet the needs and resources of individual managers, and some of the parameters that were used in the procedure were later shown to be erroneous. In addition, the Hammond system did not allow comparisons of duck use and production among lands owned by the U.S. Fish and Wildlife Service, easements by the service, and private lands. This is a critical need by managers in the prairie pothole region. With our system, we attempted to overcome some of the shortcomings of the previous system.

Here we describe a remote-sensing-based system for estimating the number and area of ponds, the sizes of breeding duck populations, and the number of young ducks recruited to the population each fall in the prairie pothole region of Minnesota, North Dakota, South Dakota, and

Montana. The area of upland habitat, number of ponds, and areas of ponds in 18 waterfowl management districts (all districts in the Dakotas and in Minnesota but only the most eastern districts in Montana) were estimated.

Our goals were to design a system that provides consistent estimates among areas and years, to maximize the use of existing data, to rapidly execute complex procedures with microcomputers, and to develop a database that documents changes in the estimated parameters.

Methods

Definitions

Definitions of the terms *wetland*, *wetland area*, *wetland basin*, and *pond* follow Cowardin (1982). We define four essential terms for describing nesting ducks: A *successful clutch* is a clutch of eggs of which one or more eggs hatch even if one or more dead young are found at the nest site (see *successful*, Klett et al. 1986). A *successful nesting attempt* is a hen's attempt to nest when that attempt results in a successful clutch. *Clutch success* is the probability that a clutch will be successful and is directly equivalent to *nest success* as defined by Klett et al. (1986). *Hen success* is the probability that a hen will make at least one successful nesting attempt during a single breeding season.

Design

The remote-sensing-based system differs from previous systems in concept, scope, and objectives. For instance, there is a relation between the amount of wetland habitat in an area and the number of ducks expected to settle there in spring. Johnson and Grier (1988) presented a rigorous discussion of the relation between numbers of ponds and numbers of ducks observed during the cooperative breeding-ground surveys. A less obvious relation is between the amount and quality of nesting habitat and the productivity of ducks (Klett et al. 1988). Direct measures of the breeding population and production are difficult and expensive. Measurements of the amount and type of habitat by remote sensing are relatively simple and inexpensive. Therefore, models that relate duck numbers and production to habitat should increase the precision of surveys without greatly increasing the cost.

Johnson et al. (1987) developed a mallard productivity model. That model and habitat data from a large sample ($n = 422$) of 10.4-km² plots and nest-survival estimates in those habitats (Klett et al. 1988) were used by Cowardin et al. (1988) to simulate results from various management scenarios. These plots and the data files from them were used as the basis for the remote-sensing-based system. From 1982 to 1986, preliminary compilation of data and tests of proposed techniques were conducted in the

Arrowwood Waterfowl Management District. The study included breeding-pair counts on 10.4-km² plots and building of baseline regression equations for estimating duck numbers from pond data. These regressions were specific to areas and years when data were available. They were later modified to account for annual and regional variations. We also assessed the adequacy of the regression equations for estimating duck numbers and evaluated video cameras.

Sample Universe

The remote-sensing-based system was applied in the prairie pothole region of the United States in Minnesota, North Dakota, South Dakota, and Montana. This area of glacial landscape is bounded on the east by forest land in Minnesota, on the south and west by the limit of glaciation in the Dakotas and Montana, and on the north by the Canadian border (Fig. 1). We approximated the boundaries by transferring boundaries presented by Hammond (1965) and Mann (1974) to 1:500,000 U.S. Geological Survey (USGS) maps with the constraint that boundaries must follow townships, which were used as a basis for stratifying sampling units.

Sample Design

The sampling units for habitat data were 10.4-km² plots. The plot size was chosen to approximate the home-range size of a breeding mallard pair (Cowardin et al. 1988). By 1990, the sample of 335 plots in 1987 was increased to 443 plots (Table 1).

The original sample was a stratified random sample of 500 plots drawn from a universe that represented the United States portion of the prairie pothole region (Cowardin et al. 1988; Fig. 2). The universe was divided into 93.2 km² townships based on 1:500,000 state maps. We defined 3 landownership classes: land owned in fee by the U.S. Fish and Wildlife Service (*service-owned land*); easements consisted of tracts for which the service obtained *easements* to prevent the draining or filling in of wetland and that included the surrounding private land in the tract; and *private land* that included private land and other state and federal land not owned by the service. Townships were assigned to 3 strata by the following rules:

- (1) A *low landownership* stratum contained 15.5 km² or less of easements and 0 km² of land owned by the service.
- (2) A *moderate landownership* stratum contained greater than 15.5 km² of easements and less than 2.6 km² of land owned by the service.
- (3) A *high landownership* stratum contained 2.6 km² or more of land owned by the service.

We randomly drew 10.4-km² plots from each landownership stratum to obtain a sample with higher sampling

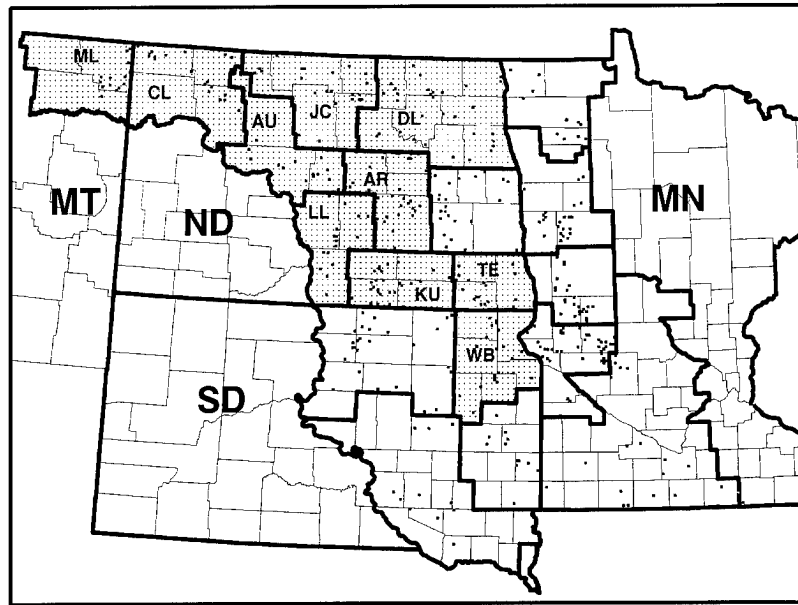


Fig. 1. Distribution of 10.4-km² sample plots ■ used to evaluate duck (Anatinae) habitat and population size during 1987–90 in the prairie pothole region of the United States. Waterfowl management districts used for analysis of duck populations are shaded. Letter codes are: AR, Arrowwood; AU, Audubon; CL Crosby-Lostwood; DL, Devils Lake; JC, J. Clark Salyer; KU, Kulm; LL, Long Lake; ML, Medicine Lake; TE, Tewaukon; WB, Waubay.

fraction in areas with high service landownership or easement because these areas were most desirable for simulations of management. At that time, recent color-infrared aerial photographs of only 422 of the selected 500 plots were available. The photographs were taken in May of a wet year. The final sample had sampling fractions of 0.0045 in the low, 0.0100 in the moderate, and 0.0824 in the high service-landownership strata. Although considered sufficiently representative for model simulations, the sample was no longer strictly random because of the plots without photographs (Cowardin et al. 1988).

We used the existing 422 sample plots as the basis for the remote-sensing-based system because of the large prior expenditure for mapping and digitizing data from those plots. This decision created three problems. First, the remote-sensing-based system required estimates by wetland management districts that were not considered in the original sample selection. Second, the method of stratification resulted in some plots without service landownership in the high or moderate landownership strata because townships

were assigned to strata and the rules did not apply to the plots. Third, when the wetland-management-district boundaries were placed over the existing sample, some waterfowl management districts contained few sample plots and some strata inside waterfowl management districts were not represented.

We re-stratified the sample to overcome the first two problems by estimating landownership in each 10.4-km² cell of the sample universe and by assigning each plot to a wetland management district. This procedure allowed us to calculate weights for each stratum and thus obtain unbiased estimates of each parameter in each waterfowl management district. The re-stratification was accomplished by mapping and digitizing all landownership classes in the entire sample universe on 1:250,000 USGS maps and by then overlaying a grid of all 10.4-km² plots. Where wetland-management-district boundaries lay along rivers, the areas were divided into irregularly shaped plots of approximately 10.4 km². This grid was digitized, and the digital data were merged with the landownership map by *The Map Overlay and*

Table 1. Numbers of 10.4-km² plots (n) for evaluating duck (Anatinae) habitat and estimating numbers of ducks and number of plots covered by videography (NV)^a during 1987–90 in the prairie pothole region of the United States.

State	1987		1988		1989		1990	
	N	NV	N	NV	N	NV	N	NV
Minnesota	95	87	98	79	128	118	128	128
Montana	14	14	14	13	14	14	14	14
North Dakota	203	202	226	219	226	220	226	223
South Dakota	23	23	23	22	75	74	75	75
All states	335	326	361	333	443	426	443	440

^a Weather conditions and time sometimes prevented acquiring video data in the required time interval.

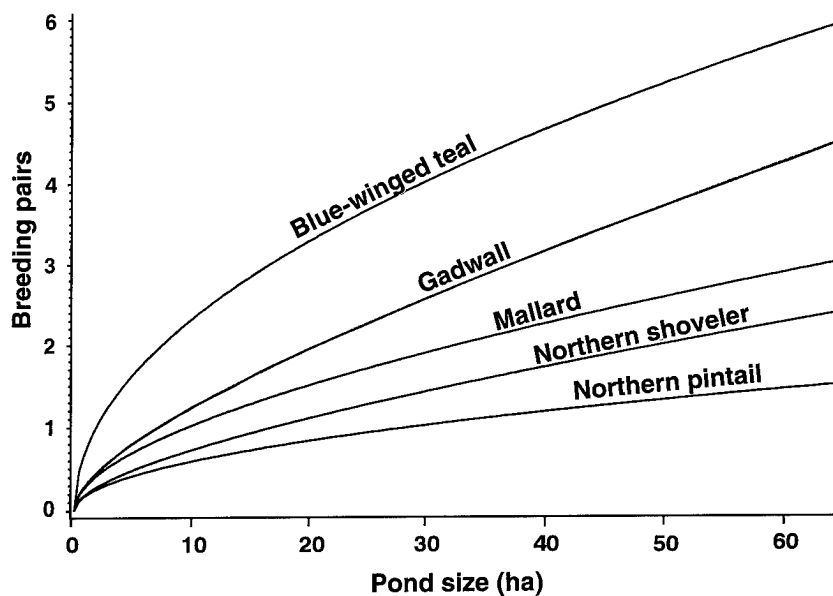


Fig. 2. Regression of number of blue-winged teal (*Anas discors*), gadwall (*Anas strepera*), mallard (*Anas platyrhynchos*), northern shoveler (*Anas clypeata*), and northern pintail (*Anas acuta*) pairs on pond size during 1987–90 in the prairie pothole region of the United States.

Statistical System (Pywell and Niedzwiedzki 1980) to produce a file with the landownership of each 10.4-km² cell in the universe. Based on these data, all plots in the universe were assigned to strata by the following rules:

1. A *refuge stratum* included any plot that contained any national wildlife refuge land regardless of other landownership in the plot.
2. A *waterfowl-production-area* stratum included any plot not classified as a refuge that included 64.8 ha or more of waterfowl production area.
3. An *easement* stratum included any plot not classified as refuge or waterfowl production area and 64.8 ha or more of service easement.
4. A *private* stratum included any plot not in the previous three strata.

In addition, each plot in the universe was assigned to the appropriate wetland management district.

To overcome the third problem, we added additional plots inside waterfowl management districts that had insufficient sample size. We required at least two sample plots in each landownership in each wetland management district. The sample contained few plots from the refuge stratum. Refuges are often larger than 10.4-km² plots, and the plot size is not well suited to obtaining a representative sample. Therefore, for this report, we collapsed refuge (stratum 1) and waterfowl production area (stratum 2) into a single stratum called *service*.

Sample Wetland Basins

Approximately 200 wetland basins were selected from all plots in each wetland management district as sites for

conducting breeding-pair counts. Sample size was determined according to the amount of time available for conducting pair counts rather than by statistical estimation of sample size required for a given degree of precision. The purpose of the pair counts was to adjust baseline regressions for annual and geographic variation in pair density. Therefore, we used an optimum allocation for a stratified random sample and treated the wetland-basin classes as strata to obtain a sample throughout the range of wetland-basin sizes and to avoid oversampling of small basins that are often dry and, therefore, provide no information about duck density. Although the technique is intended for minimizing the variance of a stratified mean, given the individual strata variances (see Neyman allocation in Cochran 1977), it also had the desired effect of reducing the sample of temporary wetland basins, which had a smaller variance than the more permanent wetland-basin classes. Strata variances were estimated from a regression model by obtaining estimates of the number of mallard pairs in each wetland basin in each plot. The area of each wetland basin was obtained from special maps prepared by the National Wetland Inventory. All wetland basins were assumed to contain ponds. Variances of the number of mallard pairs among wetland basins within each wetland-basin class in each wetland management district were then calculated.

Habitat Data

Classifications

We required a classification of wetland basins to estimate breeding duck populations and a classification of upland and wetland nesting habitat to estimate duck production.

Wetland was treated different from the other habitat classes. The National Wetland Inventory mapped wetland and upland on the plots as a special project. Wetland was mapped according to the classification and definitions in Cowardin et al. (1979) and with some exceptions according to the current mapping conventions by the National Wetland Inventory. The exceptions were that no codes for unknown water regime or mixed classes were allowed. Wetland mapping of the plots, except the addition of a unique number for each polygon in each basin, was essentially identical to the National Wetland Inventory operational inventory (Wilen 1990). Cowardin (1982) illustrated the difference between classifications of wetland area and of wetland basins. Available data for constructing pair-wetland regressions were from various basin classifications. Therefore, we had to translate the cover classes mapped by the National Wetland Inventory into basin classes. The technique was a simplification of the rules by Stewart and Kantrud (1971) for forming pond classes from wetland zones. Their pond classes (equivalent to our basin classes; Table 2) were derived from the water regime of the zone with most permanence and with an aerial cover of 5% or more. Our algorithm first summed the area of all wetland polygons in a basin by a unique identifier coded at the time of digitization. It then searched for the polygon with the most permanent water regime regardless of polygon size. If two or more polygons had the same water regime, the algorithm selected the largest. That polygon became the *basin-naming polygon* and was used to determine the class of the basin (Table 2). If the basin contained only one wetland polygon, that polygon became the basin-naming polygon by default.

Upland habitats were those described by Cowardin et al. (1988): *grassland*, *hayland*, *planted cover*, *cropland*, *woodland*, *scrubland*, *other*, *right-of-way*, and *barren land*. We modified some of the mapped habitats to obtain the nesting-habitat classes based on landownership and to reflect major habitat changes since mapping. Grassland was subdivided into *grassland* and *grassland-wildlife*. Grassland was typi-

cal pasture. Grassland-wildlife was nonuse grassland that is typical in waterfowl production areas and on refuges. Because these types are difficult to separate on aerial photographs, we defined any grassland in waterfowl production areas or refuges as grassland-wildlife. The Conservation Reserve Program of the Food Security Act of 1985 (United States Congress 1985) went into effect during our development of the remote-sensing-based system. Locations of Conservation Reserve Program tracts on 10.4-km² plots were furnished by wetland-management-district managers who obtained the locations from the county offices of the Agricultural Stabilization and Conservation Service in each wetland management district. We used the class *Conservation Reserve Program* cover for land in these tracts. Prior to analysis, we modified the corresponding habitat files for wetland management districts where we estimated duck production. The amounts of planted cover in waterfowl production areas changed from the time photographs for the National Wetland Inventory were taken and the time the plots were mapped. We obtained maps of current planted cover tracts in each wetland management district from the managers in 1987 and modified our data files to reflect current conditions. We used these data for all years irrespective of possible minor changes during 1987–90.

Habitat Maps

Habitat on each plot was interpreted, mapped, and digitized by the National Wetland Inventory. The mapping was a special project conducted for us prior to production of standard wetland maps by the National Wetland Inventory. Data were from high-altitude (1:63,360), color-infrared photographs taken during the late 1970's and early 1980's. All features on the plots were delineated with a 5-aught pen on acetate overlays. Wherever possible, areas were shown as closed polygons, but some features such as roads, trails, and rock piles had to be shown as lines or points because of the small scale. At the time of digitization, a unique basin number was added as an attribute to all polygons in a single wetland basin. Polygons, linear features, and points were transferred to 1:24,000 USGS quadrangle maps by a Bausch and Lomb Zoom Transfer Scope.

The resulting maps were then digitized on a digitizing tablet and converted to Map Overlay and Statistical System files (Pywell and Niedzwiedz 1980). A second set of 1:24,000 plot maps showing landownership boundaries was prepared from data on file at realty offices of the U.S. Fish and Wildlife Service. These maps were also digitized into Map Overlay and Statistical System files. The two Map Overlay and Statistical System files were overlaid to produce a file with the landownership attributes of all polygons. Text files of each polygon with single records were produced from these files.

Table 2. Wetland-basin class definitions based on the water regime of the basin-naming polygon.^a

Basin class	Basin-Naming Polygon
Temporary basin	Water regime temporary (a) ^b or saturated (b)
Seasonal basin	Water regime seasonal (c)
Semipermanent basin	Water regime semipermanent (f)
Lake	System Lacustrine (L) or water regime intermittently exposed (h) or permanent (g)

^a The basin-naming polygon is the polygon with the most permanent water regime in a wetland basin.

^b Letters in parentheses refer to symbols on National Wetland Inventory maps.

Because the remote-sensing-based system required that all habitats have some area, line and point features were buffered by multiplying length by average feature width (linear features) or by πr^2 (point features). The following average dimensions were determined from aerial photographs and were used for buffering linear and point data on maps: 8.2 m wide for shelterbelts; 14.6 m diameter for rockpiles and brush or grass areas, too small to enclose with a polygon; 14.6 m wide for linear wetland basins; and 15.3 m diameter for point wetland basins. Linear road features were buffered for the width of the road surface, which we equated to being barren, and for the distance from the road surface to the border of the right-of-way. Distances from the center line of the road were 3.1 m to the edge of the road surface and 10.1 m to the far edge of the right-of-way on gravel roads and respectively 3.8 m and 19.1 m on hard-surface roads and 6.1 m and 19.8 m on railroads. The average width of fence rows and vegetated strips between fields was 3.1 m.

Areas for buffered linear features and points were added to the text files derived from polygon data. This inflated the total plot area. All polygon areas were then rescaled to the true plot area by calculating a correction factor (true plot area \div inflated plot area) and by multiplying the area of each polygon by the correction factor.

Aerial Videography

The maps and databases contained data on all wetland basins (wet or dry) when the photographs were taken. We assumed that the maps had no errors from omissions or commissions. The remote-sensing-based system also required that we know the numbers and sizes of all ponds (wetland basins with water) each spring. We selected aerial video taken during flights in early May of each year as the technique to obtain these data. Video, although lacking the good resolution of photographs, has advantages over photographs (Sidle and Ziewitz 1990). Video is less expensive than aerial photography. Because a monitor is in the aircraft, the user can guide the pilot to the target area and knows whether the target area was recorded. The data are ready for immediate use at the completion of the flight. The *Map and Image Processing System* software (Miller et al. 1990) allows instant capture of the images in digital form directly from the video signal (unlike photographs, which must be scanned to produce digital data).

We used a Panasonic D 5000 video camera with a 5.9-mm Angenieux lens, a Panasonic AG 2400 video recorder, and a Panasonic CT 500V monitor. The camera was controlled by a Panasonic WVCR12 controller board. The camera was mounted in a custom-designed aluminum mount that allowed the leveling and rotation of the camera to correct for crabbing of the aircraft. The use of the short

lens did not allow use of the automatic white-balance and iris. The aperture had to be set before the flight, and the camera was white-balanced just before or during the flight.

We used several aircraft including Cessnas 172, 172RG, and 182 and a Partenavia Surveyor. A variety of camera port sizes and locations was used. Camera ports from 12.7 to 30.5 cm in diameter proved adequate, but larger ports were easier to use because the chance of including part of the aircraft skin in the video frame is less. Video data were obtained from an altitude of 3,812.5 m above ground level. This elevation combined with our type of lens permitted a 5.2-km swath width and adequate room for navigational error.

Analysis of Image Data

Video data were captured in digital form by a microcomputer with a Targa 16 image-capture board and The *Map and Image Processing System* (MIPS) software. This procedure produced a 16-bit composite raster. After capture, we classified ponds by the Feature Mapping procedure in MIPS. The objective was to classify all areas that are covered by water, including vegetation growing in water. The procedure required skill in interpretation and knowledge of local wetland conditions. The percent of the wetland basin covered by water was recorded during the counting of the breeding pairs and furnished ground truth. Feature Mapping in MIPS can be used in either an automated mode or by drawing boundaries of a pond on the screen with a mouse. Video data seldom furnish sufficient spectral separation for completely automated classification of a scene. We picked and classified training pixels, known to contain water from ground observation, until errors of commission began to appear. It was then necessary to begin on-screen interpretation by drawing boundaries around areas interpreted as wet. Where the basin contained emergent vegetation, we looked for water along the shore or in openings in the vegetation. This was a good indication of vegetation underlain by water. Sun-glint problems were resolved by referring to the original video tape and by observing sun-glint move across the scene as the aircraft moved over the wetland basin. Cloud-shadow problems were overcome by comparing the relation between the darker shading of water and the lighter shading of upland in shadows and clear areas.

Interpretation is subject to errors, and consistency among interpreters is important. Two people interpreted the same scenes of most video data to identify errors in the classification of amount of water. When inconsistencies occurred, the area was reclassified.

Duck Populations

Study Area

We restricted our analysis of annual change in ponds, duck population sizes, and duck production to 10 waterfowl

management districts (Fig. 1) for which we had aerial video data during 1987–90. Although video was obtained of other waterfowl management districts as they were added to the remote-sensing-based system, the lack of data in some years would have confounded comparisons among years.

Regression Estimates

Estimates of breeding-population sizes were derived from a regression model. Data for constructing baseline regressions for all species except wood ducks (*Aix sponsa*) were gathered at the Arrowwood Waterfowl Management District (1982–84). For wood ducks, we used data gathered at the Fergus Falls (1986–87) and Detroit Lakes (1987) waterfowl management districts. Baseline regressions were constructed by regressing the number of pairs observed on each pond on the size and the square root of the size of the pond. The general form of the equations was:

$$\text{Pairs} = A \times \text{wet area} + B \times \sqrt{\text{wet area}} \quad (1)$$

Wet area in this equation is the wet area in each pond. (Estimates of the regression coefficients A and B are presented in Table 3, and the regression curves are presented on Fig. 2).

Ground Counts

The boundary of each wetland basin where breeding-pair counts were conducted was delineated on aerial photographs, and a unique identification number for the naming of the polygon of that basin was placed on the photograph.

Table 3. Baseline regression coefficients used for estimating breeding duck (Anatinae) populations on 10.4-km² plots from the area (ha) of individual ponds determined from airborne video in the prairie pothole region of the United States, 1987–90.

Species	Regression coefficients ^a	
	A	B
Mallard	0.0106	0.2899
Gadwall	0.0341	0.2848
American wigeon	0.0000	0.0193
Green-winged teal	0.0000	0.0431
Blue-winged teal	0.0000	0.7376
Northern shoveler	0.0136	0.1870
Northern pintail	0.0000	0.1866
Redhead	0.0410	0.2233
Canvasback	0.0064	0.0453
Lesser scaup	0.0173	0.0528
Ring-necked duck	0.0022	0.0110
Ruddy duck	0.0119	0.1226
Wood duck	0.0064	0.5612

^a $\text{Pairs} = A \times \text{wet area} + B \times \sqrt{\text{wet area}}$.

The pair count was conducted by a person who walked around each pond. Pairs on lakes and rivers were sometimes surveyed from a boat or from a canoe. When dense emergent vegetation was present, the observer moved through the vegetation and flushed the birds. Sample ponds were more widely dispersed in the remote-sensing-based system than in surveys that are often conducted on plots or transects. We assumed that sample ponds were usually far enough apart to prevent the flushing of birds from one sample pond to another. Social groups were recorded on field forms designed for data entry into a microcomputer. Data were entered soon after completion of the counts. Error checking was done by a series of custom-designed programs that were executed at the time of data entry and immediately after data entry. The size of a breeding population was expressed as the estimated number of breeding pairs, which included observed breeding pairs and pairs that were inferred from other social groups. We followed approximately the same techniques described by Hammond (1969) and Dzubin (1969). The estimated number of breeding pairs was estimated by the computer at the time of data entry as follows: 1 observed pair = 1 estimated breeding pair; 1 lone male = 1 estimated breeding pair; 1 lone female diving duck = 1 estimated breeding pair; each flocked, male dabbling duck in flocks of five or fewer individuals = 1 estimated breeding pair except in wigeons and in northern shovelers for which the number of flocked males was not converted to estimated number of breeding pairs; each flocked female diving duck in flocks of five or fewer individuals = 1 estimated breeding pair. Flocked birds in flocks with more than five individuals were not used to estimate the number of breeding pairs.

Data Analyses

Estimation Procedures

We required two types of estimates: totals (e.g., number of ponds) and ratios of totals (e.g., average pond size = area of ponds per number of ponds). Where possible, we also wanted variances of these estimates.

To estimate totals, we treated our sample of 10.4-km² plots as a random sample and stratified by waterfowl management district and U.S. Fish and Wildlife Service landownership. The amount of area in a given landownership varied from plot to plot. We employed a combined ratio estimator (Cochran 1977) that made use of the fact that the totals that we wanted to estimate positively correlated with the amount of area in that landownership. Estimation was the computation of an average density by landownership from the sample plots in each waterfowl management district and the multiplication of that value by the total amount of area of that landownership in each waterfowl management district. The overlay of plots on 1:250,000 landownership maps, described under stratification, provided estimates of the amount of land by landownership in each

stratum and in each waterfowl management district. The combined totals of all landownerships were estimated by summing the landownership totals. Totals by state and their estimated variances were calculated by summing estimates from constituent waterfowl management districts.

Variances of the landownership totals were calculated with the Formula 6.51 from Cochran (1977). An upper bound to the variance of the combined total landownership of all ownership was estimated from Formula 5.10 (Cochran 1977:93).

We divided appropriate estimates of population totals of one parameter by totals of another parameter to arrive at estimates of population ratios (e.g., pairs per pond). We do not report estimated variances of population ratios because exact formulas do not exist and formulas for approximations are complex (Mood et al. 1974).

Estimates of Habitat Parameters

Number of wetland basins, area of wetland habitat, and amount of upland nesting cover were obtained from the maps of 10.4-km² plots prepared by the National Wetland Inventory. The number of ponds and the area of wetland covered by water varied from year to year and were obtained from the classified video scenes.

Number of Breeding Pairs

To estimate the size of the breeding duck population, the area of each pond (from the video scenes) was entered into the baseline regression of each species to estimate the number of the breeding pairs. These by-pond estimates were summed by plot and species and then expanded to waterfowl management districts as explained under *Estimation Procedures*. The resulting estimates were based on the assumption that the densities of ducks on ponds of the same size remains constant from year to year and from area to area. An adjustment of the differences among areas and years in each waterfowl management district was based on counts of the sample wetland basins. A correction (γ) was defined as:

$$\gamma = \frac{\text{Total number of counted pairs}}{\text{Number of pairs predicted by regression}} \quad (2)$$

To determine the number of predicted pairs in this equation, we required the area of each counted pond. The video data did not identify each pond by number. Therefore, we used the product of the estimated proportion of the basin that contained water and the mapped area of the basin to estimate the area of each counted pond. Finally, the estimated number of predicted pairs in the waterfowl management district was multiplied by γ to correct for differences in pair densities among years and among waterfowl management districts.

Estimation of Production

The number of young ducks recruited to the population in fall cannot be counted and, therefore, we used a model to calculate estimates. The model was deterministic and produced a result similar to that obtained from a stochastic mallard productivity model (Johnson et al. 1987). For our purposes, the deterministic technique was simpler and permitted more rapid calculation of estimates than the stochastic model. An example illustrates the method. To estimate the number of recruits in each landownership class, we essentially worked backwards from the general relation:

$$\text{Recruits} = 2Rn, \quad (3)$$

where 2 is a constant based on the assumption of equal sex ratio at hatch, R is the recruitment rate as defined by Cowardin and Johnson (1979), and n is the number of breeding pairs.

The recruitment rate was broken down into the components described by Cowardin and Johnson (1979) in the equation:

$$R = \frac{HZB}{2}, \quad (4)$$

where H is hen success, 2 is a constant used because recruitment is defined in terms of only females, Z is the proportion of entire broods that survived to time of census, and B is the average brood size at fledging. For mallards, we used Z = 0.74 and B = 4.9 from Cowardin and Johnson (1979). Brood survival (Z) of 0.74 was also used for gadwalls, blue-winged teals, northern shovelers, and pintails. The mallard brood size of 4.9, adjusted for broods of size zero (Cowardin and Johnson 1979), was used as baseline to estimate Class-III brood (Gallop and Marshal 1954) size of other species (Table 4).

Hen success was determined from the relation:

$$H = \alpha PE^{\alpha(1-P)^2}, \quad (5)$$

where P is clutch success, α is an index to nesting effort (Cowardin and Johnson 1979), and e is approximately 2.718. A relation between α and the percentage of basins containing water was derived from unpublished data gathered during a study of mallards in central North Dakota (Table 5). The technique was the same as that used by Cowardin et al. (1985) for relating α to the percentage of semipermanent ponds containing water. The resulting equation was:

$$\alpha = 0.616 + 0.00603 (W), \quad (6)$$

where W is the percentage of basins that contained water in a waterfowl management district, estimated from the video data and divided by total number of basins as mapped by the National Wetland Inventory.

Table 4. Average brood sizes of surface-feeding ducks (Anatinae), derived by scaling mallard (*Anas platyrhynchos*) brood size by relative clutch sizes of mallards and other species during a 1987–90 study in the prairie pothole region of the United States.

Species	Clutch size ^a	Average brood size ^b
Mallard	8.4	4.90
Gadwall	9.9	5.78
Blue-winged teal	10.2	5.93
Northern shoveler	9.9	5.78
Northern pintail	7.1	4.12

^a After Duebbert and Frank (1984:Table 3)

^b Average brood size = clutch size ÷ mallard clutch size × 4.90

Table 5. Percent of total wetland basins that contained ponds in a study area in North Dakota (Cowardin et al. 1985) and estimates of α^a during 1977–80 in the prairie pothole region of the United States.

Year	Total basins	Ponds	%	α
1977	1984	224	11.3	0.5918
1978	1984	880	44.4	0.9108
1979	1984	1527	77.0	1.0444
1980	1984	507	25.6	0.8700

^a An index to nesting intensity after Cowardin and Johnson (1979).

The number of produced recruits on a plot can be determined from the previous two equations if clutch success in each plot is available. Clutch success and the allocation of nests to the landownership classes were computed as in the following simplified example.

We assumed that the distribution of habitat and landownership (Fig. 3) was two habitats A and B and two landownerships, 259.2 ha of service landownership and

777.6 ha of private landownership. We assumed that the ducks' preference for habitat A was twice that for habitat B. If n nests were on 64.8 ha of habitat B, the number of nests on the other tracts of land could be calculated as *area of the tract ÷ 64.8 × preference value* (Fig. 3). If clutch success was assumed to be $P_A = 0.50$ and $P_B = 0.10$, we could calculate the number of successful nesting attempts in habitats A and B (Fig. 4).

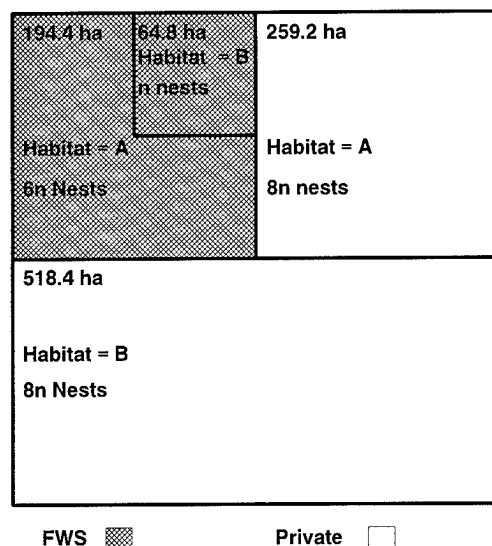


Fig. 3. Hypothetical distribution of duck (Anatinae) habitats and nests on a 10.4-km² plot with two landownerships and two habitats. Landownership classes include land owned by the U.S. Fish and Wildlife Service (service) and privately owned land (private) in the prairie pothole region of the United States, 1987–90. A and B denote arbitrary land cover types.

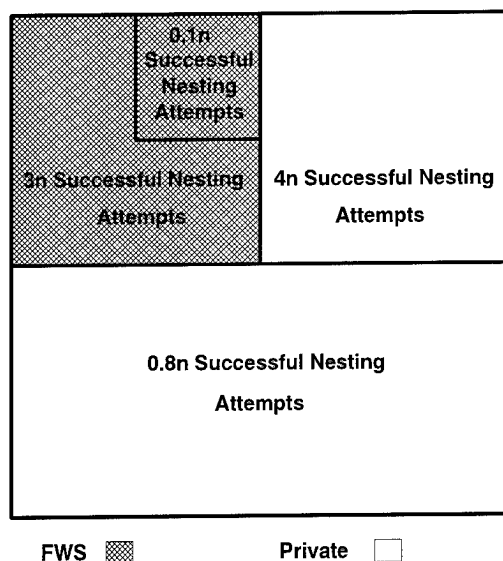


Fig. 4. Numbers of successful nesting attempts by ducks (Anatinae) on a hypothetical 10.4-km² plot with two landownerships and two habitats. Landownership classes include land owned by the U.S. Fish and Wildlife Service (service) and privately owned land (private) in the prairie pothole region of the United States, 1987–90.

With these assumptions, the total number of nests (Fig. 3) is $23n$ and the number of successful nesting attempts (Fig. 4) is $7.9n$. Therefore, the weighted clutch success in the entire plot (P) is:

$$P = \frac{\text{Number of successful nesting attempts}}{\text{Total nesting attempts}} = \frac{7.9n}{23n} = 0.34. \quad (7)$$

To allocate recruits to the landownership classes, we calculated the proportion of clutches hatched in each landownership class.

Results and Discussion

Habitat Base

The amount of land in the sample universe was 315,980 km². Most land was in North Dakota (42%), and more land was in South Dakota (29%) than in Minnesota (25%) and in Montana (5%). These values reflected the

proportions of the prairie pothole region in each state except in Montana where our data were taken from only one waterfowl management district in the northeastern part of the state and in Iowa a state that was not included in the survey. Most of the land in each state was in private landownership (Table 6). The difference among states reflected differences in the acquisition of easements rather than variation in the amount of wetland. Only about 1% of the land in the prairie pothole region is in service landownership. This land, including wetland and upland, has the greatest potential for intentional modification of habitat to benefit ducks because the service controls management.

Wetland Habitat

We estimated that about 3.1 million wetland basins covering about 28,490 km² (Table 7) were in the prairie pothole region of the United States. Most basins were in North Dakota (2.0 million), and more were in South Dakota (0.8 million) than in Minnesota (0.2 million). Our sample in Montana (48,800 wetland basins) represented only a small area of that state.

Table 6. Land ownership (%) by state in the prairie pothole region of the United States based on 1986 data.

State	Easement ^a	FWS	Private ^b
Minnesota	0.83	1.03	98.14
Montana	1.82	0.87	97.30
North Dakota	14.77	1.26	83.97
South Dakota	9.96	0.53	89.51
All States	9.37	0.97	89.65

^a Includes all land in the easement tract. Only the wetlands are under easement.

^b Includes government land not owned or under easement by the U.S. Fish and Wildlife Service.

Table 7. Estimated number of basins, area of wetland, density of basins, and area of wetland/km² by land-ownership class in the prairie pothole region of Minnesota, North Dakota, South Dakota, and extreme eastern Montana, based on photographs from the early 1980s.

State	Ownership	Number of basins		Area of wetland		Basins/km ²		Wetland ha/km ²	
		N/1000	95% CI ^a	km ²	95% CI	N. Basins	95% CI	Hectares	95% CI
Minnesota	Easement	8.6	7.5	9.8	136.1	114.5	157.7	34.7	30.1
	U.S. Fish and Wildlife Service	7.5	5.0	10.1	435.7	402.0	469.4	24.5	16.3
	Private	226.8	188.9	264.7	5,900.3	3,723.8	8,076.9	7.7	6.4
	Total	243.0	204.3	281.7	6,472.1	4,303.6	8,640.6	8.1	6.8
Montana	Easement	3.1	1.8	4.4	44.4	22.4	66.4	31.0	18.4
	U.S. Fish and Wildlife Service	0.6	0.0	2.2	81.2	31.4	131.0	13.5	0.0
	Private	45.0	26.5	63.5	449.3	146.2	752.4	8.4	4.9
	Total	48.8	29.5	68.0	574.9	210.4	939.3	8.8	5.3
North Dakota	Easement	449.5	388.9	510.1	2,387.1	2,123.1	2,651.1	59.4	51.4
	U.S. Fish and Wildlife Service	15.6	9.4	21.8	685.8	541.5	830.2	24.2	14.5
	Private	1,524.1	1,358.5	1,689.7	9,475.7	8,172.2	10,779.3	35.4	31.6
	Total	1,989.2	1,780.1	2,198.4	12,548.7	11,118.7	13,978.6	38.8	34.8
South Dakota	Easement	144.8	117.0	172.6	1,139.9	905.3	1,374.5	41.1	33.2
	U.S. Fish and Wildlife Service	2.9	1.9	3.9	257.1	194.1	320.1	15.3	9.9
	Private	662.4	563.7	761.2	7,396.9	4,821.9	9,972.0	20.9	17.8
	Total	810.1	693.5	926.7	8,793.9	6,243.8	11,344.1	22.9	29.6
All States	Easement	606.1	539.4	672.7	3,707.5	3,353.0	4,062.0	53.0	47.1
	U.S. Fish and Wildlife Service	26.7	19.7	33.6	1,459.8	1,291.2	1,628.4	22.4	16.6
	Private	2,458.4	2,261.0	2,655.7	23,222.3	19,594.7	26,849.9	22.5	20.7
	Total	3,091.1	2,847.8	3,334.4	28,389.6	24,731.3	32,047.9	25.3	23.3

^a + or - 2 standard errors.

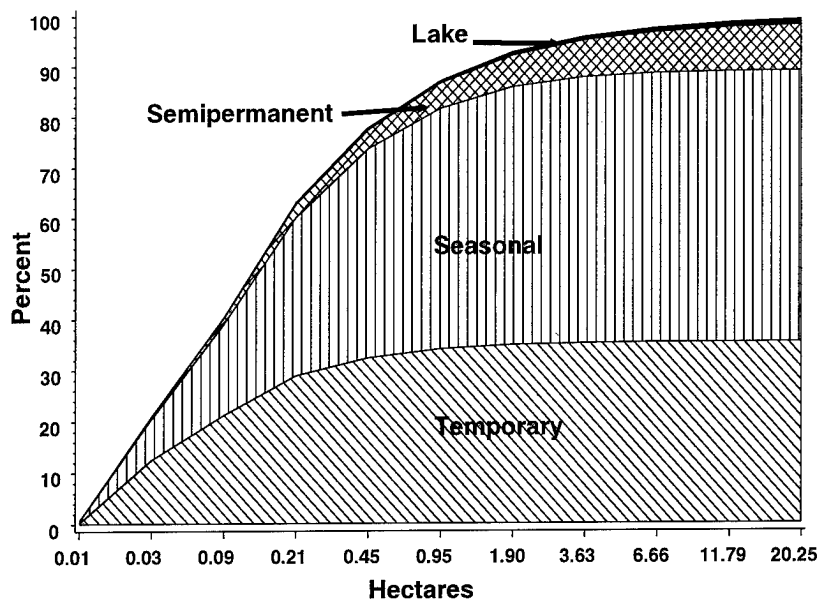


Fig. 5. Cumulative distribution of wetland basins by size and wetland-basin class in the prairie pothole region of the United States, based on photographs from the early 1980s. Wetland-basin classes include lake basins (Lake), semipermanent wetland basins (semipermanent), seasonal wetland basins (seasonal), and temporary wetland basins (temporary).

The estimated area of wetland per km^2 was similar among the states except in Montana where the area was about half of that in other states. The estimated density of wetland basins varied among states. The highest density was in North Dakota. The estimated mean wetland-basin sizes were 2.7 ha in Minnesota, 1.2 ha in Montana, 0.6 ha in North Dakota, and 1.1 ha in South Dakota. The distribution of wetland basins by size class was highly skewed to the smaller sizes (Fig. 5). This distribution was biased because parts of some wetland basins on the plot boundary included only the area inside the plot. The bias was greatest in areas of large lakes. The estimated wetland area per km^2 was greater on service easements than on private land and was

much greater on service-owned land than in any of the other landownership classes because the service tended to buy large wetland basins, especially for refuges. Estimated wetland-basin density was highest on service easements (Table 7) because easements were taken in areas of high wetland-basin density and the wetland basins were small.

The distribution of wetland-basin classes varied by landownership class (Fig. 6). The distributions of wetland-basin classes on easements and on private land were similar, except more seasonal wetland basins and fewer lakes were on easements than on private land. Temporary and seasonal wetland basins were greatly underrepresented and lakes were overrepresented on service-owned land most of which

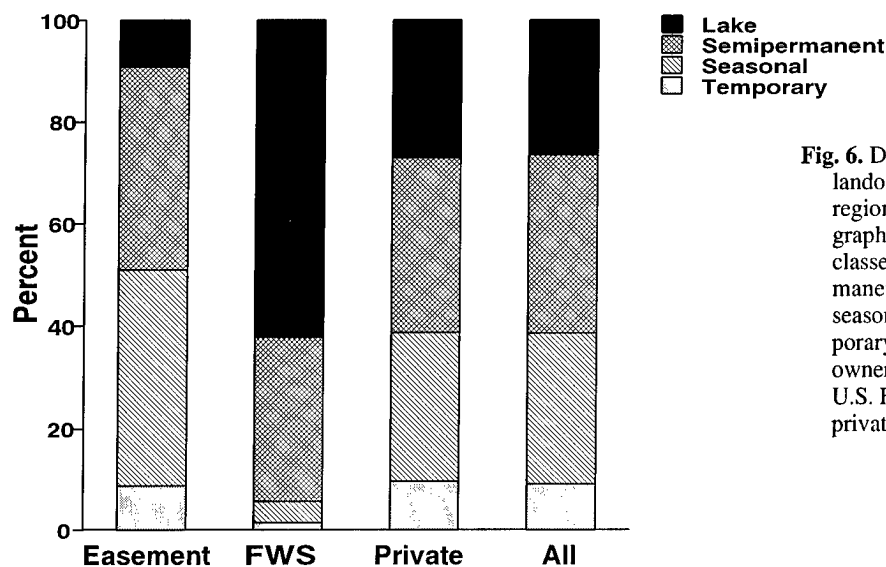


Fig. 6. Distribution of wetland-basin classes by landownership class in the prairie pothole region of the United States, based on photographs from the early 1980s. Wetland-basin classes include lake basins (lake), semipermanent wetland basins (semipermanent), seasonal wetland basins (seasonal), and temporary wetland basins (temporary). Landownership classes include land owned by the U.S. Fish and Wildlife Service (service) and privately owned land (private).

is on refuges, which were historically purchased as resting areas for migrating birds and not as waterfowl production areas.

Upland Habitat

The estimated area of upland-habitat classes (Table 8) varied by state and landownership class. Cropland was the dominant land-cover class on private land and on easements in all four states. The distribution of area of land-cover classes on easements and on private land was similar. The small amount of cropland on service-owned land was the result of tillage on some refuges and in waterfowl production areas where tillage was used to rejuvenate planted cover or to provide food plots. These tilled areas appeared as cropland on aerial photographs.

Grassland was the second most abundant component of the landscape in all states and its abundance increased from east to west. The percent of grassland was lowest in Minnesota (6.7) and lower in North Dakota (16.3) than in South Dakota (26.0) and in Montana (33.9). The distribution of grassland-wildlife (Table 8) was partly an artifact of our definition. No grassland was shown on service-owned land and no grassland-wildlife was shown on easements and on private land. The occurrences of hayland and other land were minor but were important duck nesting habitat (Cowardin et al. 1985). Planted cover was uncommon except on service-owned land where it was a major habitat component.

Annual Change in Ponds

Pond density varied from $4.4/\text{km}^2$ in 1987 to 0.8 in 1990 (Fig. 7). The area of ponds (ha per km^2) varied from 7.2 in 1987 to 2.7 in 1990 (Fig. 8). Climate in the prairie pothole region occurs in cycles of wetness and drought (Kentrud et al. 1989). Near-average water conditions were present in 1987 and followed by drought in 1988, slight recovery in 1989, and severe drought in 1990. The highest density of ponds was on easements, especially in 1987 (Fig. 7). The area of ponds per km^2 was greater on service-owned land than in the other types of landownership (Fig. 8). Although these large basins with semipermanent water regimes responded more slowly to drought conditions, surface water declined steadily throughout the period (Fig. 8). The area of ponds per km^2 on easements and on private land fluctuated similarly. The average pond size (Fig. 9) increased slightly as the amount of surface water declined because small wetland basins dried up entirely. The average pond size in wetland basins on service-owned lands increased during 1987–88, contracted as small ponds appeared in 1989, and increased again in 1990 as the small ponds again disappeared. The average pond size was less in 1990 than in 1988 because even the larger ponds were becoming smaller because of severe drought.

Duck Populations and Production

Breeding Populations

The 13 duck species reported here (Fig. 10) represent 39% of the duck species that breed in North America and 73% of the species in the genera *Anas* and *Aythya* in North America. During 1987–90, the density of the blue-winged teal ($3.4 \text{ pairs}/\text{km}^2$) was higher than those of the mallard, (2.1), gadwall (1.8), northern pintail (0.8), and redhead (0.8) (Fig. 11). Density was consistently highest on service-owned lands primarily because of the large areas of ponds.

Annual Change in Sizes of Breeding Populations

The sizes of the breeding populations of the five most numerous dabbling ducks declined throughout 1987–90 as drought conditions intensified (Fig. 11). The declines corresponded closely to loss of ponds (Fig. 7) and pond area (Fig. 8), but the relation of pair density to area of ponds differed by species (Fig. 12). We expected species with a high degree of philopatry and possibly weak territoriality to concentrate on ponds as the number of ponds decreased because of drought. Slopes of the linear regressions of pair density on pond density (Fig. 13) were: -0.108 (gadwalls), -0.098 (mallards), -0.071 (blue-winged teals), -0.025 (northern shovelers), and -0.0004 northern pintails). The ranking is similar to published data on return rates (Anderson et al. 1992). Mallards and gadwalls exhibit strong philopatry (Lakemoen et al. 1990). Our ranking of blue-winged teals is higher and of northern pintails lower than expected according to the literature. The comparison with the literature can only be approximate because of considerable spatial and temporal variations in published return rates, variation of return rates by age and sex, and rare correction of published return rates of mortality.

Our data (Fig. 12) may suggest that, where the correlation between the area of ponds and breeding population is low, the number of ducks is too low to fill the available breeding habitat. However, other explanations are possible, and we found no data that support a depression of northern shoveler populations. Johnson and Shaffer (1987) analyzed data from annual surveys by the service and concluded that estimated mallard population sizes no longer parallel estimated pond numbers. Their first possible explanation was that the number of mallards was too low to fill the habitat.

Change in the total number of pairs per km^2 by year varied among landownership classes (Fig. 14). The highest density was on service-owned land as expected because more wetland and more pond area are on these lands than on land in the other landownership classes. The decrease in pairs per km^2 during 1987–88 was less severe on service-owned lands than on other lands, probably because of the greater amount of semipermanent

Table 8. Estimated area of upland habitats by landownership class in the prairie pothole region of Minnesota, North Dakota, South Dakota, and extreme eastern Montana, based on photographs from the early 1980s.

State	Ownership	Area of barren land			Area of cropland			Area of grassland			Area of grassland-wildlife		
		km ²	95%	CI ^a	km ²	95%	CI	km ²	95%	CI	km ²	95%	CI
Minnesota	Easement	4.3	2.7	5.8	340.0	302.6	377.3	61.6	38.5	84.6	0.0	0.0	0.0
	U.S. Fish and Wildlife Service	1.1	0.3	1.9	55.6	30.2	81.0	0.0	0.0	0.0	47.6	28.8	66.3
	Private	2,396.4	1,080.1	3,712.7	54,401.2	51,170.1	57,632.4	5,162.9	3,494.2	6,831.8	0.0	0.0	0.0
	Total	2,401.8	1,085.9	3,717.6	54,796.8	51,557.4	58,036.2	5,224.5	3,560.9	6,880.1	47.6	28.8	66.3
Montana	Easement	0.6	0.3	0.8	106.4	65.2	147.6	108.9	79.1	138.7	0.0	0.0	0.0
	U.S. Fish and Wildlife Service	0.1	0.0	0.2	2.1	0.0	5.4	0.0	0.0	0.0	38.3	0.0	78.3
	Private	113.8	62.8	164.8	8,449.2	5,452.6	11,445.9	4,735.6	1,608.7	7,862.5	0.0	0.0	0.0
	Total	114.4	63.1	165.6	8,557.7	5,544.0	11,571.5	4,844.5	1,709.1	7,979.9	38.3	0.0	78.3
North Dakota	Easement	117.2	96.0	138.4	11,294.9	10,564.0	12,025.6	4,693.0	3,837.0	5,549.0	0.0	0.0	0.0
	U.S. Fish and Wildlife Service	1.1	0.2	2.0	217.2	116.0	318.4	0.0	0.0	0.0	443.9	311.2	576.7
	Private	2,743.6	896.0	4,591.2	73,693.1	69,709.9	77,676.4	16,957.2	14,648.4	19,266.0	0.0	0.0	0.0
	Total	2,861.9	1,007.5	4,716.3	85,205.2	80,939.8	89,470.6	21,650.2	18,958.7	24,341.7	443.9	311.2	576.7
South Dakota	Easement	61.2	28.5	93.9	4,302.5	3,260.4	5,344.7	2,984.9	2,269.3	3,700.5	0.0	0.0	0.0
	U.S. Fish and Wildlife Service	0.3	0.1	0.6	50.6	13.8	87.5	0.0	0.0	0.0	93.6	62.2	125.1
	Private	1,601.1	1,438.5	1,763.6	45,427.7	41,448.8	49,406.7	20,779.7	17,720.2	23,839.2	0.0	0.0	0.0
	Total	1,662.6	1,509.7	1,815.5	49,780.8	45,518.4	54,043.3	23,764.5	20,486.0	27,043.1	93.6	62.2	125.1
All States	Easement	183.2	144.2	222.2	16,043.7	14,769.7	17,317.8	7,848.4	6,732.1	8,964.7	0.0	0.0	0.0
	U.S. Fish and Wildlife Service	2.6	1.3	3.8	325.5	214.8	436.2	0.0	0.0	0.0	623.4	480.0	766.9
	Private	6,854.9	4,579.9	9,129.8	181,971.3	174,821.6	189,121.0	47,635.4	42,414.8	52,855.9	0.0	0.0	0.0
	Total	7,040.6	4,761.2	9,320.1	198,340.6	190,861.4	205,819.8	55,483.7	49,952.8	61,014.7	623.4	480.0	766.9
State	Ownership	Area of hayland			Area of other habitat			Area of planted cover			Area of right-of-way		
		km ²	95%	CI ^a	km ²	95%	CI	km ²	95%	CI	km ²	95%	CI
Minnesota	Easement	15.2	5.2	25.1	67.8	53.0	82.5	20.1	3.4	36.7	0.0	0.0	0.0
	U.S. Fish and Wildlife Service	2.8	0.0	7.3	37.7	22.4	52.9	216.5	170.9	262.0	0.0	0.0	0.0
	Private	2,057.7	1,525.2	2,590.3	4,336.7	3,535.0	5,138.4	119.2	55.3	183.2	1,621.0	1,335.7	1,906.3
	Total	2,075.7	1,541.7	2,609.6	4,442.1	3,628.5	5,255.7	355.7	260.7	450.8	1,621.0	1,335.7	1,906.3
Montana	Easement	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0
	U.S. Fish and Wildlife Service	0.0	0.0	0.0	0.0	0.0	0.3	3.8	0.0	18.2	0.0	0.0	0.0
	Private	1.9	0.0	5.7	62.6	25.3	100.0	3.1	0.0	8.6	103.7	34.1	173.2
	Total	1.9	0.0	5.7	63.0	25.7	100.2	6.9	0.0	19.9	103.7	34.1	173.2

North Dakota	Easement	582.3	382.1	782.5	398.5	339.2	457.7	103.3	0.0	218.9	14.0	2.5	25.5
	U.S. Fish and Wildlife Service	1.5	0.0	4.7	113.2	0.0	231.4	202.7	105.7	299.7	2.6	0.4	4.8
	Private	2,490.2	1,850.4	3,130.2	3,849.2	2,122.1	5,576.3	293.5	157.0	430.0	1,881.0	1,625.3	2,136.8
	Total	3,074.1	2,365.2	3,782.9	4,360.8	2,492.9	6,228.7	599.4	369.2	829.7	1,897.6	1,636.4	2,158.8
South Dakota	Easement	448.5	115.3	781.6	139.3	92.2	186.5	41.4	0.0	95.0	0.7	0.0	2.3
	U.S. Fish and Wildlife Service	3.9	0.0	8.1	7.6	2.8	12.4	73.3	20.1	126.4	0.0	0.0	0.0
	Private	3,188.6	1,895.0	4,482.1	2,022.2	1,504.2	2,540.3	220.0	0.0	466.5	1,329.0	1,011.5	1,646.7
	Total	3,640.9	2,270.3	5,011.5	2,169.1	1,647.4	2,690.8	334.7	56.4	613.1	1,329.8	1,005.4	1,654.2
All States	Easement	1,045.9	657.1	1,434.7	605.9	528.7	683.0	164.8	36.3	293.2	14.7	3.1	26.3
	U.S. Fish and Wildlife Service	8.3	1.4	15.2	158.4	39.1	277.7	496.2	375.7	616.7	2.6	0.4	4.8
	Private	7,738.4	6,200.1	9,276.7	10,270.7	8,297.1	12,244.4	635.9	346.9	924.9	4,934.8	4,432.2	5,437.3
	Total	8,792.5	7,159.7	10,425.4	11,035.0	8,931.6	13,138.4	1,296.8	923.1	1,670.5	4,952.0	4,438.5	5,465.6

a + or - 2 standard errors.

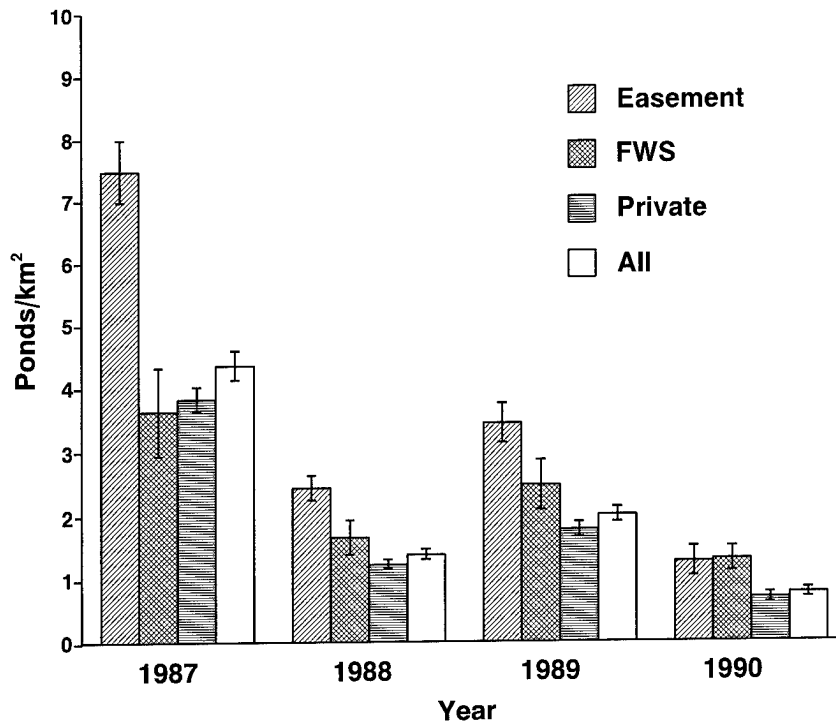


Fig. 7. Density of ponds by landownership class during 1987–90 in the prairie pothole region of the United States, based on aerial videography. Landownership classes include easements (easement) where the U.S. Fish and Wildlife Service has easements on wetlands to prevent draining, filling, or leveling; land owned by the U.S. Fish and Wildlife Service (service); privately owned land (Private); and all landownerships combined (all). Error bars = 1 standard error.

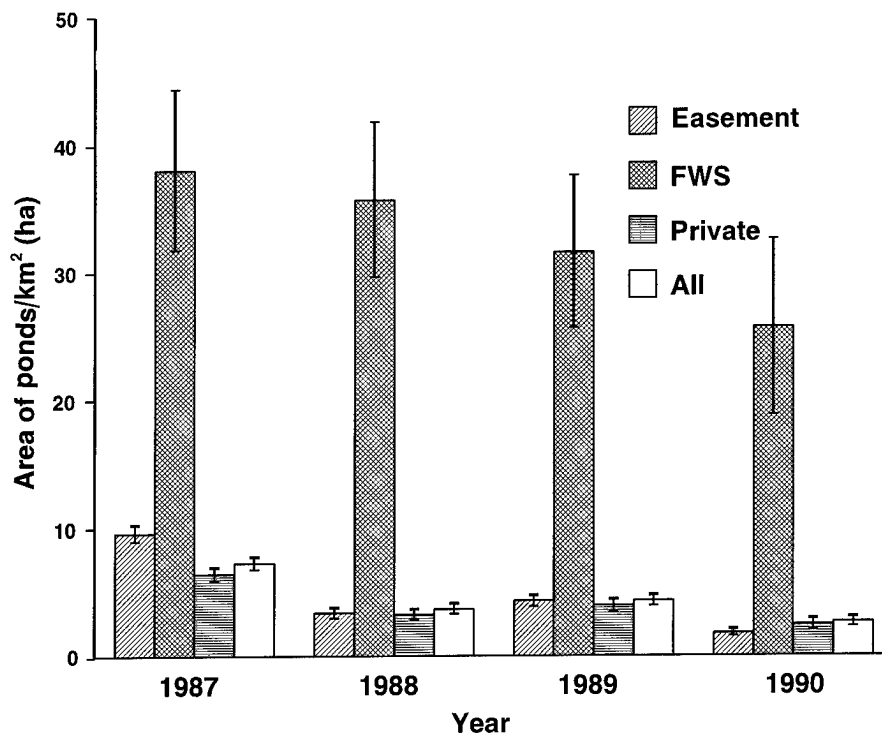


Fig. 8. Area of ponds per km² by landownership class, during 1987–90 in the prairie pothole region of the United States, based on aerial videography. Landownership classes include easements (easement) where the U.S. Fish and Wildlife Service has easements on wetlands to prevent draining, filling, or leveling; land owned by the U.S. Fish and Wildlife Service (service); privately owned land (private); and all landownerships combined (All). Error bars = 1 standard error.

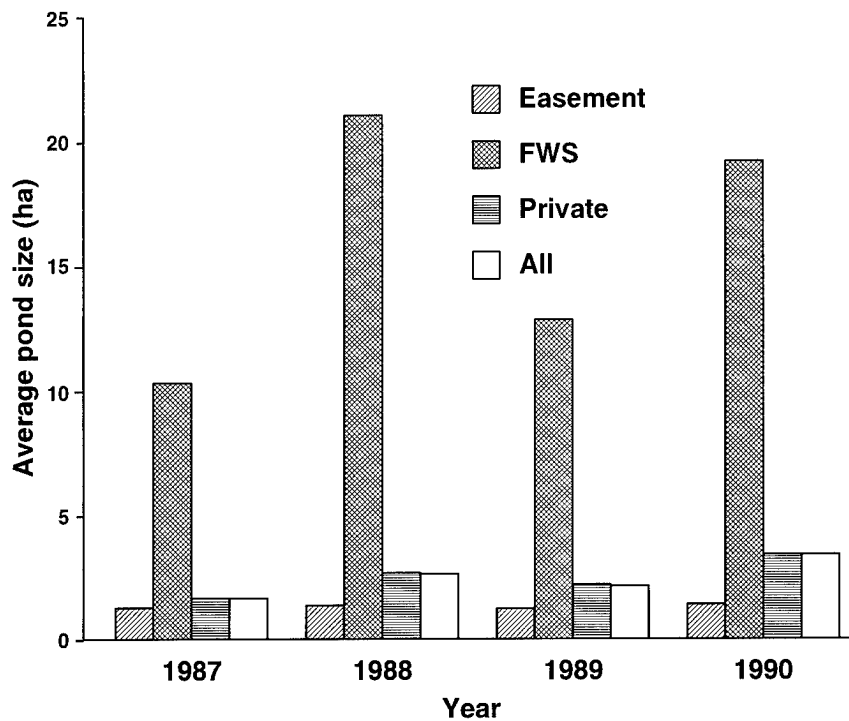


Fig. 9. Average size of ponds by landownership class during 1987–90 in the prairie pothole region of the United States, based on aerial videography. Land-ownership classes include easements (easement) where the U.S. Fish and Wildlife Service has easements on wetlands to prevent draining, filling, or leveling; land owned by the U.S. Fish and Wildlife Service (service); privately owned land (private); and all landownerships combined (all). 1987–90.

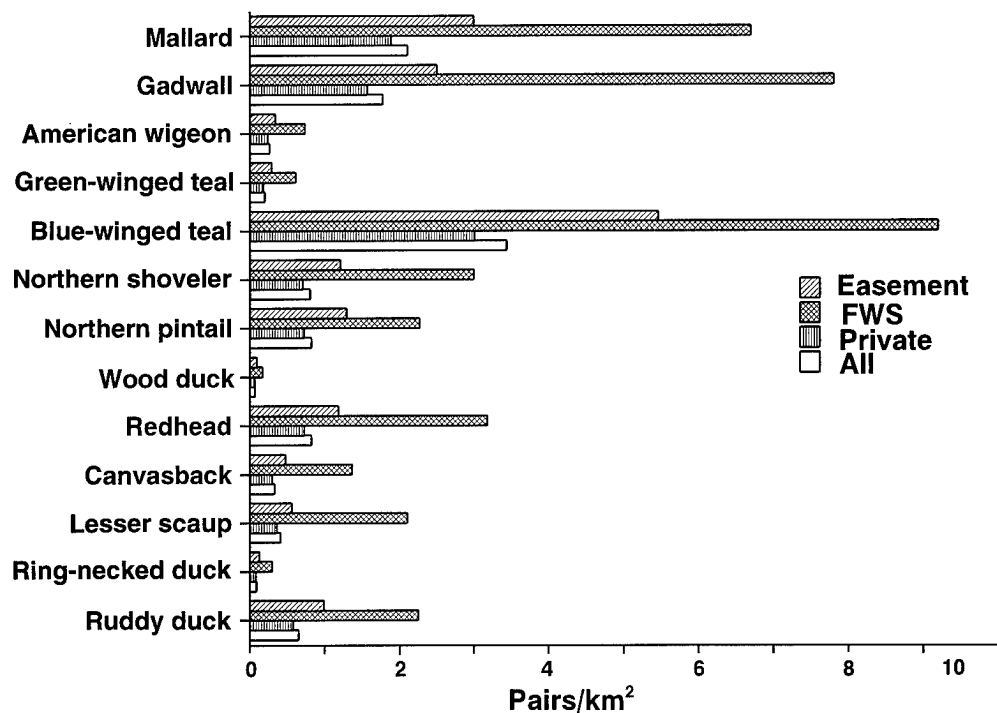


Fig. 10. Average density of breeding ducks (Anatinae) by landownership class during 1987–90 in the prairie pothole region of the United States, based on model projections from aerial videography and ground counts. Duck species include mallards (*Anas platyrhynchos*), gadwalls (*Anas strepera*), American wigeons (*Anas americana*), green-winged teals (*Anas crecca*), blue-winged teals (*Anas discors*), northern shovelers (*Anas clypeata*), northern pintails (*Anas acuta*), wood ducks (*Aix sponsa*), redheads (*Aythya americana*), canvasbacks (*Aythya valisneria*), lesser scaups (*Aythya affinis*), ring-necked ducks (*Aythya collaris*), and ruddy ducks (*Oxyura jamaicensis*).

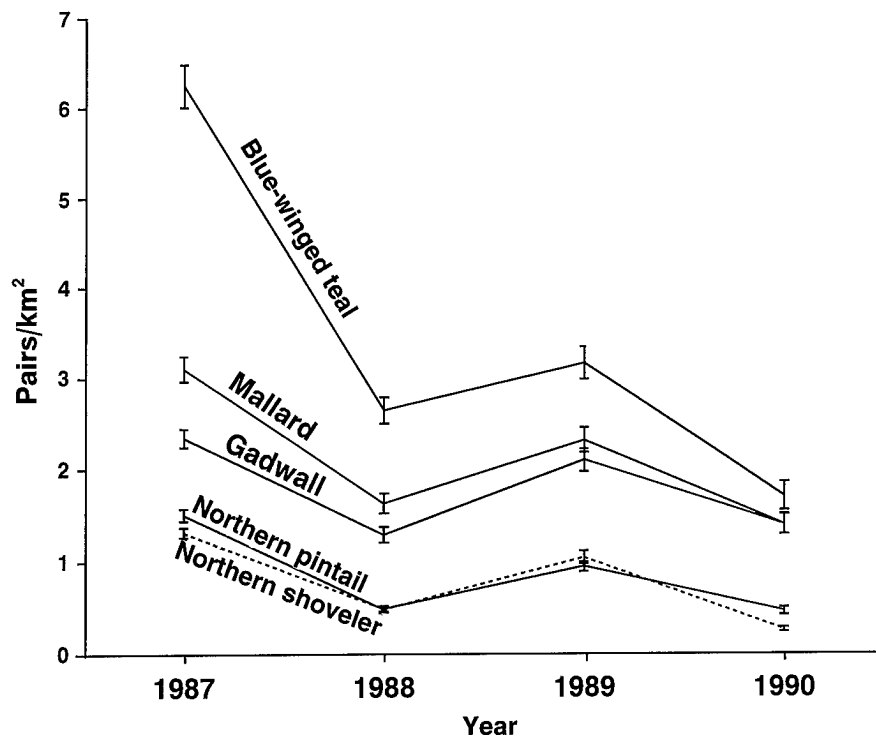


Fig. 11. Relation of density of blue-winged teal (*Anas discors*), gadwall (*Anas strepera*), mallard (*Anas platyrhynchos*), northern shoveler (*Anas clypeata*), and northern pintail (*Anas acuta*) pairs to pond size during 1987–90 in the prairie pothole region of the United States. Error bars = 1 standard error.

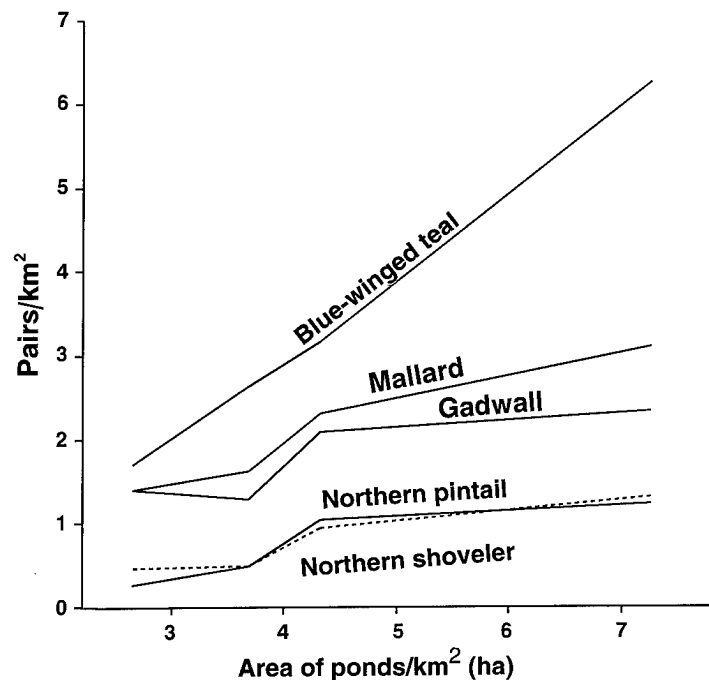


Fig. 12. Relation between density of blue-winged teal (*Anas discors*), gadwall (*Anas strepera*), mallard (*Anas platyrhynchos*), northern shoveler (*Anas clypeata*), and northern pintail (*Anas acuta*) pairs to area of ponds during 1987–90 in the prairie pothole region of the United States.

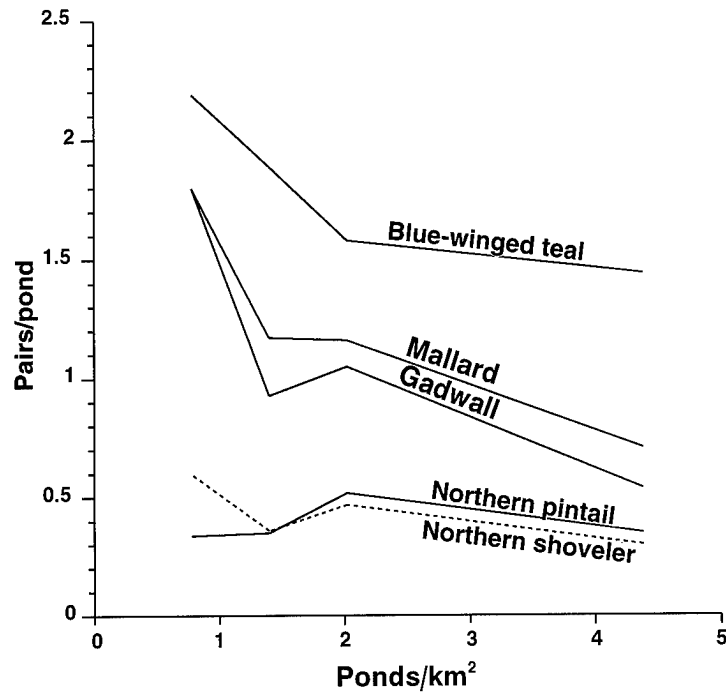


Fig. 13. Relation between average number of pairs of blue-winged teals (*Anas discors*), gadwalls (*Anas strepera*), mallards (*Anas platyrhynchos*), northern shovelers (*Anas clypeata*), and northern pintails (*Anas acuta*) per pond and pond density during 1987–90 in the prairie pothole region of the United States.

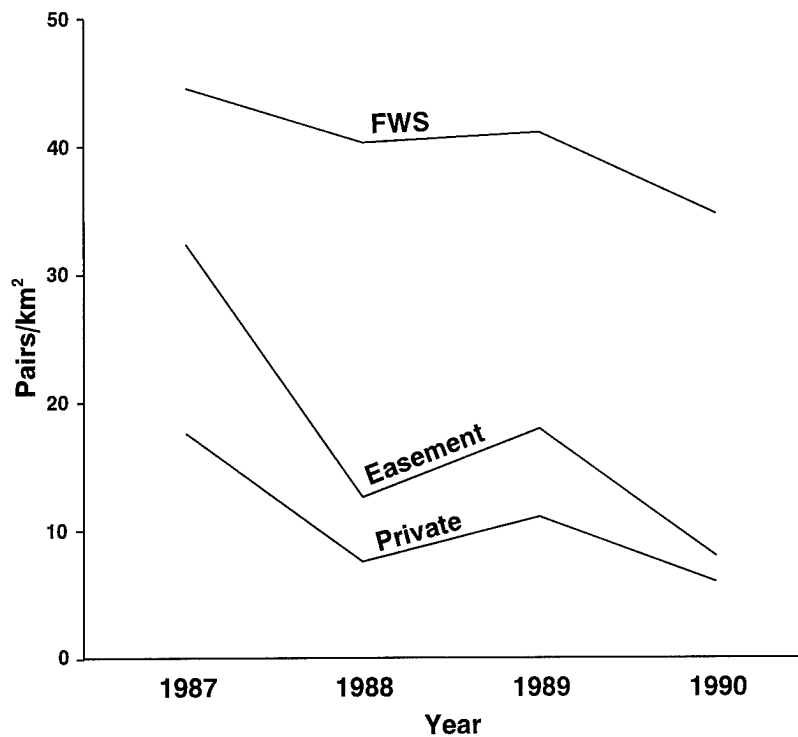


Fig. 14. Relation between the average number of duck (Anatinae) pairs per km² and year by landownership class during 1987–90 in the prairie pothole region of the United States. Landownership classes include easements (easement) where the U.S. Fish and Wildlife Service has easements on wetlands to prevent draining, filling, or leveling; land owned by the U.S. Fish and Wildlife Service (service); privately owned land (private).

wetland basins on service-owned land. Birds that return to a landscape in a drought, where the less permanent ponds were dry, probably concentrated on large semipermanent wetland basins like those on service-owned land. The decline of the number of pairs was more apparent on easements than on private lands. More wetland basins are on easements than on private lands, but not as many large semipermanent and permanent wetland basins are on easements as on private lands (Fig. 8).

Duck Production

The number of recruits is the product of size of breeding population and the recruitment rate (Cowardin and Johnson 1979). Drought has a negative effect on both (Cowardin et al. 1985, Johnson and Grier 1988). We point out that our estimated recruitment rate was more dependent on model prediction than on observation and was highly influenced by the underlying assumptions of the model. The estimated density of the recruited ducklings (Fig. 15) followed the same general pattern as the sizes of the breeding populations among the five species (Figs. 10 and 15) and among years (Figs. 11 and 16) of the five species for which production was estimated. The estimated recruitment rates varied among species and among years (Fig. 17). The rates were highest in blue-winged teals and gadwalls and lowest in mallards and northern pintails. The annual variation in recruitment rates (Fig. 17) resulted from variation in α (a measure of nesting intensity; Table 9). Our estimates of α had a major effect on our estimates of hen success (Equa-

tion 5). The estimated clutch success in stable populations (Cowardin et al. 1985 and Klett et al. 1988) is lower than those presented in Table 10. However, the estimates presented in those papers were based on the assumption that α equaled 1. For the low α values in this study, higher clutch success is required for recruitment rates of a stable population. For mallards, a hen success of 31%, a summer survival of 0.74, and an average brood size of 4.9 (Cowardin et al. 1985) equate to a recruitment rate of 0.56 in a stable population. This is well above our estimated recruitment rate in mallards (Fig. 17).

We did not have sufficient data for estimating clutch success by year. Greenwood et al. (1995) showed that clutch success in the prairies of Canada is depressed by drought. If we had estimates of clutch success by year, the variation in our estimated recruitment rate by year (Fig. 17) would probably have been greater.

Our model predicted that the densities of mallard, gadwall, blue-winged teal, and northern shoveler recruits were greater on service-owned land than on easements and private land (Fig. 16). Northern pintail recruits were produced at almost equal rates in the landownership classes. The number of successful nesting attempts per km² varied by landownership class (Fig. 18) because of the differences in clutch success (Table 10) and the relative preferences of the different species for the various nesting habitats (Klett et al. 1988, Table 2) on those lands. Klett et al. (1988) found a higher preference for cropland in northern pintails than in other duck species. The densities of successful nesting

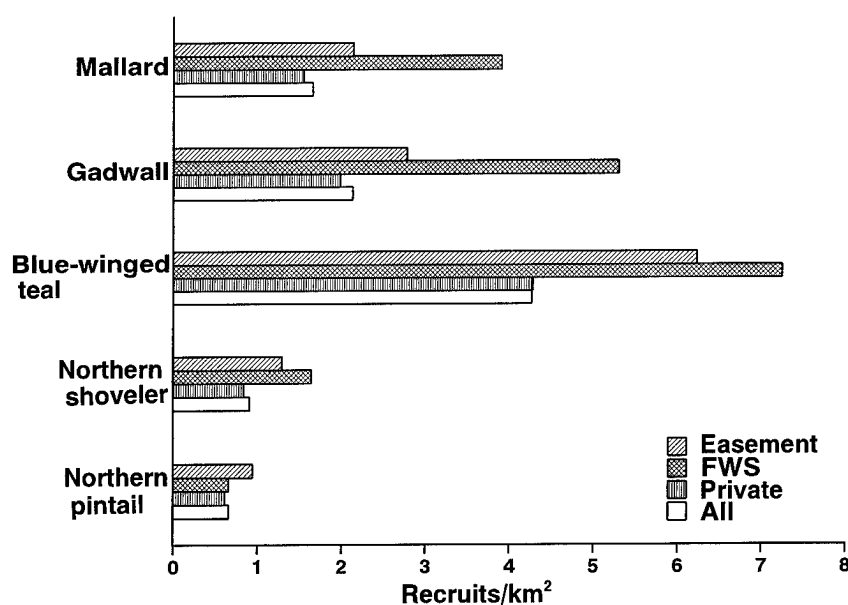


Fig. 15. Number of produced recruits per km² by mallards (*Anas platyrhynchos*), gadwalls (*Anas strepera*), blue-winged teals (*Anas discors*), northern shovelers (*Anas clypeata*), and northern pintails (*Anas acuta*) during 1987–90 in the prairie pothole region of the United States, based on model projections from aerial videography and ground counts. Landownership classes include easements (easement) where the U.S. Fish and Wildlife Service has easements on wetlands to prevent draining, filling, or leveling; land owned by the U.S. Fish and Wildlife Service (service); privately owned land (private); and all landownerships combined (all). 1987–90. Error bars = 1 standard error.

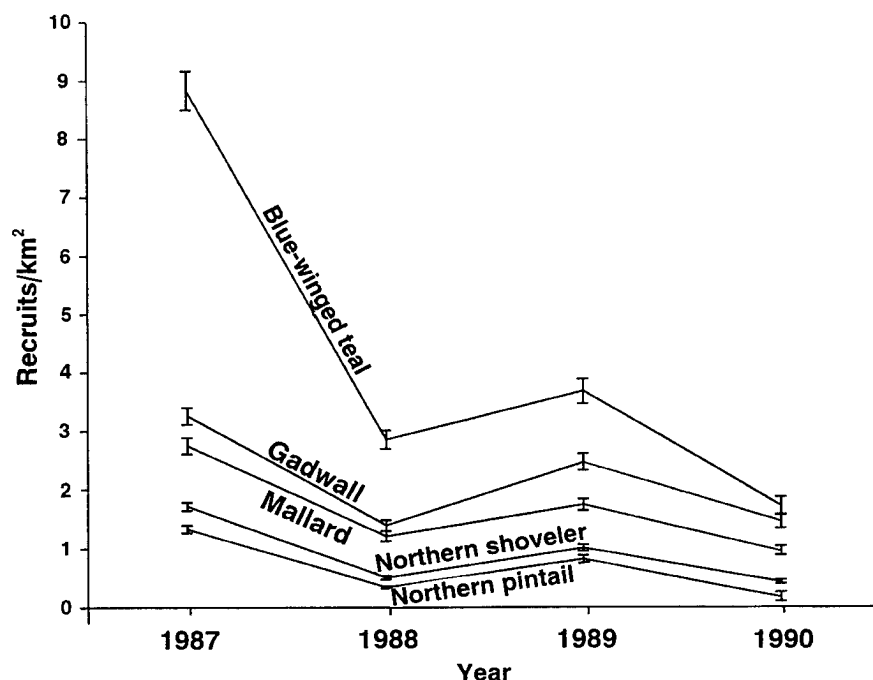


Fig. 16. Number of produced recruits per mi^2 of blue-winged teals (*Anas discors*), gadwalls (*Anas strepera*), mallards (*Anas platyrhynchos*), northern shovelers (*Anas clypeata*), and northern pintails (*Anas acuta*) during 1987–90 in the prairie pothole region of the United States, based on model projections from aerial videography and ground counts. Error bars = 1 standard error.

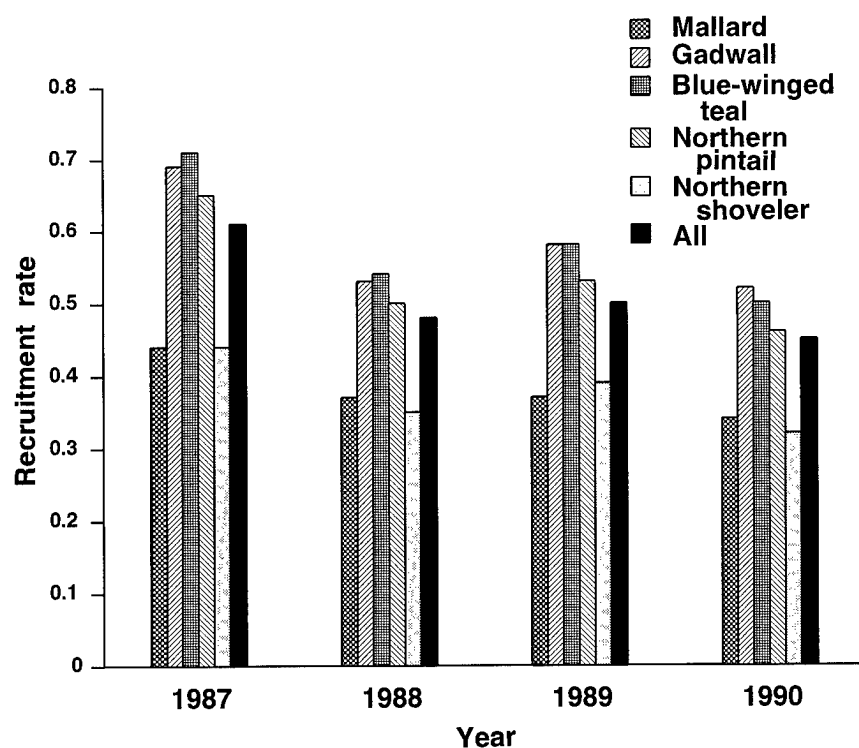


Fig. 17. Recruitment rate of five species of dabbling ducks during 1987–90 in the prairie pothole region of the United States, based on model projections from aerial videography and ground counts. Species include mallards (*Anas platyrhynchos*), gadwalls (*Anas strepera*), blue-winged teals (*Anas discors*), northern shovelers (*Anas clypeata*), and northern pintails (*Anas acuta*) and all species combined.

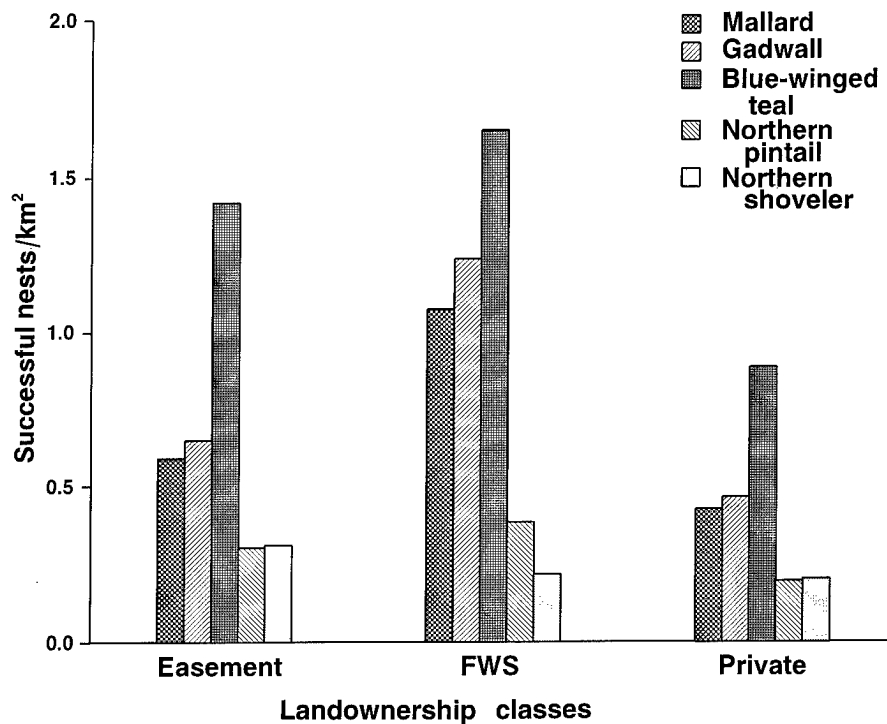
Table 9. Estimates of α , a measure of nesting intensity, by wetland management district and year during 1987–90 in the prairie pothole region of the United States.^a

District	1987	1988	1989	1990
Arrowwood	0.962	0.776	0.711	0.668
Audubon	0.858	0.721	0.655	0.640
Crosby-Lostwood	0.736	0.655	0.729	0.629
Devils Lake	0.745	0.650	0.656	0.642
J. Clark Salyer	0.744	0.658	0.654	0.630
Kulm	0.879	0.673	0.759	0.657
Long Lake	0.920	0.701	0.678	0.640
Medicine Lake	0.820	0.669	0.844	0.697
Tewaukon	0.741	0.751	0.766	0.676
Waubay	0.803	0.684	0.844	0.745

^a α is a linear function of the percentage of wetland basins containing water in each year.

Table 10. Estimates of average clutch success by species and landownership class during 1987–90 in the prairie pothole region of the United States.

Species	Ownership			
	Easement	FWS	Private	All Owners
Mallard	17	22	17	17
Gadwall	22	27	24	24
Blue-winged teal	22	23	23	23
Northern shoveler	21	21	21	21
Northern pintail	20	21	21	21
All species	20	24	21	21

**Fig. 18.** Average number of successful nesting attempts per km² by mallards (*Anas platyrhynchos*), gadwalls (*Anas strepera*), blue-winged teals (*Anas discors*), northern shovellers (*Anas chryseata*), and northern pintails (*Anas acuta*) by landownership class in the prairie pothole region of the United States, based on model projections from aerial videography and ground counts. Landownership classes include easements (easement) where the U.S. Fish and Wildlife Service has easements on wetlands to prevent draining, filling, or leveling; land owned by the U.S. Fish and Wildlife Service (service); and privately owned land (private).

attempts per km² in mallards, gadwalls, and blue-winged teals were higher on service-owned lands than on other lands. The number of successful nesting attempts per km² by northern pintails and northern shovelers was similar among the landownership classes.

Conclusions and Management Implications

Wetland and Duck Management

The Effect of Service-owned Land

Sidle (1983) described how alarm over declining duck populations and destruction of prairie-pothole wetland habitat led to the service's small wetland acquisition program (DeBates 1967). Our data demonstrated how waterfowl production areas and service easements acquired under this program and national wildlife refuges are important. These lands not only prevent further destruction of wetland but also provide areas where ducks can continue to reproduce. If these lands can be managed so that recruitment rate more than compensates for annual mortality, the managed lands may slow or reverse the declines of some duck populations. In 10 waterfowl management districts, service-owned land was only 1.3% of the land surface, but 2.5% of the five most common dabbling ducks were produced on it. On easements, including the wetlands under easement and the private land in the easement tract, 19.6% of the ducks were produced on 14.1% of the land surface. Private land on the other hand produced 77.9% of the ducks on 84.6% of the land surface. These estimates do not include the contribution of service-owned land and easements where the preserved wetlands contribute to duck production from surrounding private uplands. Thus, lands owned in fee and easements taken on wetlands increase duck production; however, most ducks are produced on private lands.

The people who initiated the small wetland-acquisition realized that bigger and wetter wetland is not necessarily better for ducks. Kaminski and Weller (1992) summarized results from several studies that revealed the importance of seasonal wetlands to dabbling ducks. These wetlands are generally small. The cumulative frequency distribution of wetland basins by size class in the prairie pothole region (Fig. 5) has important management and conservation implications. Restricting regulatory responsibility or protection to larger basins would leave most of the prairie potholes unprotected. For example, 78% of the basins are less than 0.41 ha and most have temporary or seasonal water regimes.

Wetland easements are the main source of protection for wetland basins with temporary and seasonal water regimes because these classes are poorly represented on lands owned in fee title (Fig. 6). The large lakes on national wildlife

refuges may serve as resting areas for migrating waterfowl, but their contribution to duck production is minor.

Drought Effects

Our estimates from the remote-sensing-based system during the first 4 years clearly supported the well known fact that drought depresses duck populations and production in the prairie. Data gathered during this period revealed only the decline in breeding populations as drought conditions increased during 1987–90. Data gathered in future years may document the increase in populations and production as water conditions improve on the prairies. Although the large wetland basins on service-owned lands contribute little to duck production, our data suggested that, because they may remain wet during drought, large wetland basins with permanent water regimes may modify drought effects.

Species Effects

Duck management is often based on mallards because data are more comprehensive on mallards than on other duck species. The assumption is that management that is good for mallards is good for other ducks. The assumption is probably valid for some dabbling ducks, but managers should be aware of species differences. Our analysis agreed with published information on philopatry (Lokemoen et al. 1990), which suggests that homing to natal areas is stronger in mallards and gadwalls than in the other species we studied. This means that intensive management to increase local recruitment would be more beneficial to these species than to those that do not home strongly.

The analysis of successful nesting attempts per km² by landownership class (Fig. 18) revealed additional important species differences from the interaction of preferences for nesting covers, clutch success in the various covers, and the types of cover in the landownership classes. Accordingly, management of uplands to benefit mallards and gadwalls on service-owned lands may not be beneficial to northern pintails and northern shovelers. Upland management probably has limited value for diving ducks, most of which nest in wetlands. Management of service-owned lands and easements to preserve wetland may have a beneficial effect by providing nesting areas for diving ducks and for some dabbling ducks, especially in dry years.

System Evaluation

Possible Biases

The estimates derived from the remote-sensing-based system may have several biases. Testing for these biases requires special studies that were beyond the scope of our evaluation. Typical difficulties in estimating duck numbers and production over vast areas may preclude objective veri-

fication. Our purpose here is to alert the reader to some of the more important possible sources of errors.

The remote-sensing-based system is based on data from remote sensing for the identification of wetlands and uplands from aerial photographs and on data from aerial video for measuring annual change in the number of ponds and area of water. We made the assumption that mapping by the National Wetland Inventory was without errors of omission or commission. Although not tested, our experience in this and numerous other studies in the prairie pothole region revealed that such errors are few. Errors that we detected were usually errors of omission of small temporary wetland basins. These errors lead to underestimation of breeding-population sizes. Data on the number of ponds and on the area of water from video (sometimes poor quality) may contain errors from the omission of numbers of ponds (L. L. Strong, Northern Prairie Science Center, National Biological Service, Jamestown, N. Dak., unpublished data). These errors cause the underestimation of breeding-population sizes. They also cause the underestimation of α and, therefore, recruitment rate. We also point out that our method for estimating α relies on data from only 4 years in one study. We also make the assumption that the form of the regression curves for estimating the number of breeding pairs is the same among years and areas. This assumption was not examined. Adjustment of regressions by γ may have introduced errors that we are currently unable to evaluate.

For the estimates of duck production, we used Conservation Reserve Program cover estimates from 1990 and applied them to all years. Conservation Reserve Program contracts were taken during 1987–90. Conservation Reserve Program cover is attractive to ducks with relatively high clutch success (Kantrud 1993, Reynolds et al. 1994); therefore, our estimates of production in years prior to 1990 may be high.

All systems for the estimation of breeding-population sizes of ducks are subject to errors of biological interpretation such as determining whether an observed pair of ducks represents a resident or migrant pair and whether observed social groups such as lone males represent breeding pairs (Cowardin and Blohm 1992). We made no attempt to solve these problems but attempted to use methods that correspond to those used in other surveys so that the estimates are comparable.

Sampling Errors

Although our overall sample size (Table 1) was large, samples in some wetland-management-district-landownership strata were small, and variation in habitats among plots was great. Confidence limits on most estimates of habitat parameters were large. Cost probably prohibits large increases of sample size, although addi-

tional plots are currently added to the sample where sample sizes are minimal. At present, wetland mapping and digitizing in the entire prairie pothole region are progressing rapidly, and technology is available for adding uplands to the data. When data from the entire prairie pothole region become available, sampling will no longer be necessary for estimating numbers of wetland basins and wetland area. Our confidence limits for duck-population sizes and duck-production parameters reflect only the variation associated with our sample of 10.4-km² plots. For example, the confidence limits do not reflect the variance in the number of ducks or recruitment in individual plots. Thus, the confidence limits for these parameters are actually narrower than they should be.

Suggested Future Modifications

The remote-sensing-based system, although operational, should be considered a prototype that can be improved by various modifications and by the addition of new data. One simple modification would be a complete inventory of wetlands as described in the previous section. Annual estimation of the number of ponds will probably have to remain sample based because of cost and logistic problems in obtaining complete remote-sensing data over such a large area each spring. Satellite data with sufficient resolution to delineate the small ponds that ducks use may become available at a reasonable cost in the future, but obtaining data in the required narrow time frame will remain a problem. Advances in aerial videography techniques have been made since the remote-sensing-based system was initiated. We recommend that new methods be evaluated to increase the accuracy of the annual estimates of the number of ponds. We used ratio-estimation methods involving the amount of land area in each landownership class to improve our estimates of several parameters. Ratio estimates involving area of wetland or numbers of basins in each landownership class could further improve estimates of parameters such as area and number of ponds or numbers of breeding pairs. Such improvements will be possible when the inventory of wetlands is complete.

As use of the remote-sensing-based system continues, new data become available for improving the regression equations for estimating numbers of breeding pairs from pond areas. Furthermore, the classification of wetland basins should be modified to better represent major differences in duck use. For example, the current class *lakes* includes many types of lakes that receive different use by ducks. The data should be examined to determine whether enough information exists to construct regressions for various kinds of lakes. In addition, the remote-sensing-based system was designed primarily for estimating numbers of pairs on discrete basins. The remote-sensing-based system does not work well for estimating numbers of pairs

on large lakes and in riverine habitat. Studies should be conducted to determine whether shoreline segments of lakes and reaches of rivers are preferable sampling units in these habitats. Such a change requires gathering data from these units to develop appropriate regression models for the remote-sensing-based system.

When we designed the remote-sensing-based system, we could not link vector data from the National Wetland Inventory maps to the raster data from aerial videography. Therefore, ground crews estimated the proportion of a wetland basin containing water. These estimates were used to calculate γ . The link between the two data sets is now available, and we recommend that aerial videography (or possibly photography) be used for determining γ .

Overall Assessment of the System

Our first goal with the remote-sensing-based system was consistency of estimates among areas and years. We believe that this goal was accomplished, although major differences in habitat among waterfowl management districts demand some regional modification of methods. Our second goal was maximum use of existing data. We believe that this objective was accomplished, but implementation of the remote-sensing-based system clearly pointed out that certain data required by the system are scarce or lacking. This is especially true for reliable estimates of clutch success in some areas and in some habitats (Shaffer and Newton, in press). Our third goal was rapid execution of complex procedures by microcomputer and a resulting database that documents changes in the estimated parameters. This goal was partly accomplished. Because the remote-sensing-based system has been constantly evolving, continued modification of computer programs has been necessary. At the same time, technological advances in computer development and remote-sensing techniques have moved ahead of those used in the remote-sensing-based system.

Fluctuation—sometimes violent—of breeding-population sizes and production of prairie ducks causes problems for waterfowl managers. The manager usually attempts to manage such things with the amount and extent of harvest and the availability and quality of habitat. The success or failure of management is usually evaluated in terms of duck numbers and production. Johnson and Shaffer (1987) demonstrated the difficulty of separating weather factors from the numerous other causes of fluctuation in duck population sizes and the need for long-term surveys with consistent methodology. The remote-sensing-based system proposed here has the potential to provide better evaluation of management by providing data that are essential to understanding the interaction of various factors that cause fluctuation in duck population sizes.

Acknowledgments

This study was a cooperative effort by research personnel of the Northern Prairie Wildlife Research Center and managers in Regions 3 and 6 of the U.S. Fish and Wildlife Service. Numerous individuals from the waterfowl management districts assisted with pair counts and in the later years with conducting the aerial video missions. In addition, the regions furnished financial support. Mapping of the plots and management of digital files were done by R. Gebhard and H. R. Pywell of the National Wetland Inventory. C. R. Luna assembled landownership data on maps that were then digitized by the National Wetland Inventory. Lab technicians J. Belant, D. Hertel, P. S. Marshall, and H. T. Sklebar photointerpreted video images and maintained data files during development of the remote-sensing-based system. In 1990, video interpretation and data management became the responsibilities of the Habitat and Population Evaluation Teams of the U.S. Fish and Wildlife Service in Bismarck, North Dakota, and in Fergus Falls, Minnesota. R. C. Khan-Malek wrote computer programs and assisted with the preparation of figures. H. T. Sklebar processed digital images. D. H. Johnson furnished advice throughout the study and initiated work on pair wetland regressions and on the productivity model that are integral parts of the remote-sensing-based system. J. E. Austin, N. H. Euliss, D. H. Johnson, W. E. Newton, R. T. Reynolds, and A. B. Sargeant kindly reviewed earlier drafts of the manuscript.

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A list of current *Biological Science Reports* follows:

1. Reproduction and Distribution of Bald Eagles in Voyageurs National Park, Minnesota, 1973-1993, by Leland H. Grim and Larry W. Kallemeyn. 1995. 28 pp.

U.S. Department of the Interior National Biological Service

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This responsibility includes fostering the sound use of our lands and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities.

